Bilateral Asymmetry in Skeletal Growth and Maturation as an Indicator of Environmental Stress

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ABSTRACT This study examined the efficacy of bilateral asymmetry in epiphyseal union as an indicator of environmental stress affecting the skeleton. We compared the extent of asymmetry in the postcranial skeleton between two cemetery samples excavated from Medieval Kulubnarti, Sudanese Nubia. Past studies have strongly suggested that these ancient Nubians experienced environmental stress—the early Christian period (550–750 AD) population to a greater extent than the late Christian period (750–1450 AD) population. We hypothesized that if bilateral asymmetry is a reflection of stress, then it should be present or greater in the more stressed population, the early Christian period population, while absent or found to a lesser extent in the less stressed population, the late Christian period population.

We computed two mean values, representative of right-side and left-side epiphyseal union, for each individual in both cemetery samples, and tested for significant differences. Bilateral asymmetry was significant in the combined cemetery sample of 90 individuals ($P < 0.019$). When cemetery samples were tested separately, bilateral asymmetry was significant for the early Christian period sample ($P < 0.001$), but not for the late Christian period sample. There were no differences attributable to sex. Finally, we discuss why we conclude that environmental stress was favored over a biomechanic explanation as the cause for asymmetry. To the extent that our results support previous findings that early Christian period individuals were more affected by environmental stress than late Christian period individuals, it is reasonable to consider bilateral asymmetry in skeletal growth and maturation a good indicator of environmental stress. Am J Phys Anthropol 110:341–349, 1999.

The purpose of this study was to examine bilateral asymmetry in postcranial skeletal growth and maturation for its potential use as an indicator of environmental stress. We documented the stages and progress of epiphyseal union of paired bones from a skeletal sample for which stress has been well established—from Medieval Kulubnarti, Sudanese Nubia—and tested for significant differences between right- and left-side development. We hypothesized that the early Christian period (550–750 AD) cemetery sample would show significant differences in bilateral asymmetry, whereas the late Christian period (750–1450 AD) cemetery sample would show no significant bilateral asymmetry, given that past studies support that the late Christian period population was less stressed than the early Christian period

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population (Van Gerven et al., 1981; Hummert, 1983; Hummert and Van Gerven, 1983; Sanford et al., 1983; Van Gerven et al., 1985; Moore et al., 1986; Sheridan, 1992; Mittler and Van Gerven, 1994; Sanford and Kissling, 1994).

The examination of dental and skeletal asymmetries has been used as a means of assessing the level of developmental stability in various organisms. Developmental stability refers to the ability of an organism to grow and mature in a steady manner, to its phenotypic potential, under a wide variety of environmental conditions (Moller, 1997). Developmental stability is also referred to as developmental homeostasis. Developmental homeostasis is viewed as a reflection of the degree to which an organism's genotype allows for the rise of an adaptive phenotype when confronted with environmental perturbations (Livshits and Kobyliansky, 1991). Environmental perturbations are likely causes of disruptions in developmental homeostasis, which in turn may manifest as skeletal and or dental bilateral asymmetry.

When the skeletal and dental asymmetry does not favor one side of the body over the other, it is termed fluctuating asymmetry (FA) (Perzigian, 1977; Van Valen, 1962). Directional asymmetry (DA) appears when there is differential development favoring one side of the body consistently over the other. Antisymmetry (AS) indicates the presence of asymmetry, but with variability in terms of which side of the body is affected more than the other (Van Valen, 1962).

Many studies support the argument that environmental stress effects, and not genetics or lower degrees of heterozygosity, cause FA in the skeleton and dentition (Byers, 1997; Corruccini et al., 1982; Guagliardo, 1981; Kieser et al., 1997; Leamy, 1997; Livshits and Kobyliansky, 1991; Mack et al., 1995; Moller, 1977; Parsons, 1990; Perzigian, 1977; Van Valen, 1962). Moreover, biomechanic forces have been offered as a cause of DA in limb bone structure (Roy et al., 1994; Ruff and Jones, 1981). In addition to biomechanic factors, Helmkamp and Falk (1990) draw attention to age- and sex-related ontogenetic factors in causing DA. Other studies discuss the difficulty in determining if skeletal asymmetry is more affected by environmental factors or genetic factors (Foundas et al., 1998; Trinkaus, 1978). Certain types of DA have been attributed to genetics, such as the occlusal morphology of the first permanent molar studied by Pirttiniemi et al. (1998). But, Pirttiniemi et al. (1998) also discuss findings of increased bilateral asymmetry in the dentition of laboratory animals after exposure to stress during development.

Studies concerning either FA or DA in the skeleton and dentition can be grouped into three broad categories based on their focus. First, dental and skeletal asymmetries have been studied to ascertain their range of variation, naturally existing (de Araujo et al., 1994a; Mowbray, 1994) or resulting from adaptations to functional demands (Huggare and Houghton, 1995). Second, dental asymmetry has been studied as an indication of disease, trauma, or abnormality. For example, asymmetry evidenced as dental malocclusions has been examined, whereby malocclusions were attributed to dental deviations and not skeletal dysplasias (de Araujo et al., 1994b; Rose et al., 1994). Dental asymmetry has also been tested as a possible diagnostic feature of temporo-mandibular-joint disease (TMJ) (Kenworthy et al., 1997). Lastly, Halgrimsson (1995) conducted a study to assess the cause of fluctuating dental and skeletal asymmetry, which led to the finding that increases in asymmetry were related to increases in maturational spans (i.e. the time it takes to mature) in primate—especially hominoid—evolution, and not differences in body size.

The phenomenon of bilateral asymmetry, whether fluctuating or directional, assuredly has varying implications depending on the focus of study. We were interested in exploring the existence of either FA or DA in epiphyseal union of paired bones as a means of demonstrating stress in teenage and young adult skeletons. Goodman et al. (1984) proposed a model for understanding stress in the skeleton in which they discussed three skeletal indicators of general and cumulative stress: growth assessment, dental asymmetry, and mortality. We propose that differences in the timing and sequence of epiphyseal union between right and left

sides of paired bones (i.e., a form of growth assessment) may indicate stress in a manner similar to dental asymmetries.

Generally, the dentition could be viewed as more resistant to the effects of environmental stress than the postcranial skeleton. For example, Smith et al. (1982) found no significant increase in FA in metric measures of the dentition of children who had experienced prenatal stresses. Moreover, dental formation typically correlates more highly with age at death than does epiphyseal union (Ubelaker, 1987), which suggests that dental formation is under tighter genetic control, and or perhaps influenced less by environmental factors than is epiphyseal union. Therefore, it is likely that bilateral asymmetries in epiphyseal union may exist in skeletons where dental asymmetries do not.

Inasmuch as Kulubnarti skeletons were examined in this study, it is noteworthy that meaningful interpretations of dental metric asymmetry in the Kulubnarti populations were not available. Although dental metric asymmetries were studied, conclusions about their meaningfulness were not possible due to limitations with the F-Ratio statistic when used on sample sizes less than 120. Further, there was a consideration as to the likely confounding effect resulting from typical measurement error, which can artificially inflate variance (i.e. asymmetry measures) (Greene, 1984).

Another important concern is the veracity of interpreting significant differences in bilateral asymmetry as the result of environmental stress as opposed to normal human variation. Baer and Durkatz (1957) studied asymmetry in the hand and wrist from radiographs of 245 modern, healthy children. They found no statistically significant differences in maturation of one hand or wrist over the other, nor were there differences between females and males. Moreover, there was less variability and less bilateral asymmetry found in the epiphyses of the hand as opposed to the greater variability and greater bilateral asymmetry found for the onset of ossification. Baer and Durkatz suggest that the level of bilateral asymmetry evident in a population of normal, healthy children is the result of variability in the timing of ossification. Bilateral asymmetry in the hand bones, therefore, could be seen as variation in the rate of maturation. But statistically significant bilateral asymmetry leads to questions concerning what factors other than genetics might influence variation in ossification.

Baer and Durkatz refer to early studies (such as Todd, 1937; Francis and Werle, 1939; Francis, 1940; Pyle et al., 1948; Mann et al., 1948) that have emphasized the importance of metabolic disturbances, disease, and chronic nutritional deficiencies in causing maturational delays. Based on the work of Baer and Durkatz and their discussion of earlier studies, it appears as though normal human variation in bilateral skeletal maturation consistently does not yield statistically significant asymmetry differences. Thus, if bilateral asymmetry in skeletal maturation is statistically significant, it is reasonable to explore the role of some sort of environmental perturbation.

MATERIALS AND METHODS

Sample

The early and late Christian period cemetery skeletons (550–1450 AD) excavated from Kulubnarti, Sudanese Nubia, were ideal for this study in that 1) environmental stress had been previously demonstrated (Van Gerven et al., 1981; Hummert, 1983; Hummert and Van Gerven, 1983; Sanford et al., 1983; Van Gerven et al., 1985; Moore et al., 1986; Sheridan, 1992; Mittler and Van Gerven, 1994; Sanford and Kissling, 1994), and 2) there were numerous well-preserved, nearly complete skeletons ranging from young adolescence to young adulthood. Ages were originally estimated for earlier research using dental eruption and epiphyseal union for subadults, and seriation techniques based primarily on morphological changes in the pubic symphysis, followed by dental attrition and osteoarthritic changes for adults (Van Gerven et al., 1981; Moore et al., 1986). Sex estimations had been previously determined via pelvic morphology or by soft tissue remains where possible.

A total of 90 individuals, from developmental ages 11 to 31 years, comprised the sample. There were 36 individuals from the early Christian period (550–750 AD) cem-

etery sample (12 females, 8 males, and 16 indeterminate), and 54 individuals from the late Christian sample (750–1450 AD) period cemetery (25 females, 18 males, and 11 indeterminate). Although the fusion activity of most epiphyses peaks during the teenage years and into the early 20s, the sample included individuals aged 11 to 31 years to account for the possibility of premature or delayed skeletal growth and maturation.

Data collection

Stages of epiphyseal union were assessed via gross examination, and recorded for the following paired skeletal sites: medial and lateral epicondyles and proximal and distal epiphyses of the humerus, proximal and distal epiphyses of the radius, ulna, femur, tibia, and fibula; anterior iliac crests and ischial tuberosities of the innominates; and the medial clavicular epiphyses. We employed a four-stage method of scoring the progress of fusion of epiphyses: 0 for no union (with or without a separate epiphysis present), 1 for beginning union or union in progress (where less than half of the epiphysis is fused), 2 for nearly complete union or recent union (where more than half of the epiphysis is fused, or where the line of union is still clear and marked), and 3 for complete union (where fusion has been complete for some time such that only a scar may be seen, if there is any mark left at all). This scoring method, used in studies by Albert (1993) and Albert and Maples (1995), is a modification of McKern and Stewart's (1957) scoring method.

Asymmetry variables and reliability

Asymmetry variables were determined by computing two mean values for each of 90 individuals in the sample, one for right-side epiphyseal union and one for left-side epiphyseal union. Stages of epiphyseal union were recorded as whole numbers, or as ordinal-level data. The computing of mean values allowed for a conversion of the data from ordinal-level to ratio-level, which permitted the use of *t*-tests. Since one mean value is actually an average, if a stage of epiphyseal union is arguable (i.e. Stage 1 vs. 2, or Stage 2 vs. 3), this one difference would not greatly impact the overall mean, which in turn would not affect the overall pattern of asymmetry being evaluated.

Significant differences between right-side and left-side epiphyseal union mean values were to be interpreted as the result of some type of environmental influence, and not due to measurement error. Fields et al. (1995) address the problem of attributing FA to environmental stress. They raise the issue of measurement error being a likely confounding factor in the attempt to quantify asymmetry. Fields et al. suggest a direct test of reliability coefficients for asymmetry measurements, or the use of statistical tests that account for measurement error.

Smith et al. (1982) point out that large sample sizes are necessary to detect fluctuating dental metric asymmetries where small differences exist. They also note that the type of statistic employed causes differences in estimates of fluctuating dental metric asymmetry. Further, there is also the problem of measurement error. Kieser and Groeneveld (1991) and Keiser et al. (1990) studied the reliability of dental measures, and suggested that a large part of error in human dental mensuration is due to interobserver bias.

Our study, however, entailed documenting four stages of the progress of epiphyseal fusion as opposed to discrete metric measures of any kind. We collected ordinal-level data where four whole numbers represented four increasingly advancing stages of union. The magnitude of the difference from one stage to the next could not be quantified. Rather, each higher stage meant a greater extent of maturity. The reliability of the scoring method we used is supported by an earlier interobserver bias test of the same method of scoring epiphyseal union.

Albert (1993) conducted an interobserver bias test on the scoring method used in this study. An analysis of variance was computed for four independent observers and the mean reliability ranged from 0.96 to 0.99. We believe that any evidence of significant bilateral asymmetry found in this study could indeed be attributable to a real phenomenon of environmental stress rather than some confounding effect in measurement error. That environmental stress, and not some

TABLE 1. Paired samples t*-tests for bilateral asymmetry in epiphyseal union by population*

Sample	Pair	N	Mean	SD	SEM	*t*	df	Sig. two-tailed
Early and Late Christian period	RMEAN-LMEAN	90	−6.21E-02	.2459	2.592E-02	−2.395	89	.019
Early Christian period	RMEAN-LMEAN	36	−8.06E-02	.1319	2.199E-02	−3.666	35	.001
Late Christian period	RMEAN-LMEAN	54	−4.97E-02	.2994	4.075E-02	−1.220	53	.228

RMEAN, right-side epiphyseal union mean; LMEAN, left-side epiphyseal union mean.

TABLE 2. Paired samples t*-tests for bilateral asymmetry in epiphyseal union by sex*

Sample	Pair	N	Mean	SD	SEM	*t*	df	Sig. two-tailed
Early and Late Christian period								
Female	RMEAN-LMEAN	37	4.580E-02	.2578	4.239E-02	1.080	36	.287
Male	RMEAN-LMEAN	26	−5.25E-02	.1466	2.874E-02	−1.825	25	.080
Early Christian period								
Female	RMEAN-LMEAN	12	−4.72E-03	.1405	4.056E-02	−.116	11	.910
Male	RMEAN-LMEAN	8	7.473E-02	.1605	5.676E-02	−1.317	7	.229
Late Christian period								
Female	RMEAN-LMEAN	25	7.004E-02	.2980	5.959E-02	1.175	24	.251
Male	RMEAN-LMEAN	18	4.256E-02	.1437	3.386E-02	1.257	17	.226

RMEAN, right-side epiphyseal union mean; LMEAN, left-side epiphyseal union mean.

other factor such as biomechanics, explains asymmetry is addressed later.

Epiphyseal union data for the paired skeletal sites were consolidated into two variables representative of bilateral asymmetry: right-side and left-side epiphyseal union mean. These two asymmetry variables were not used as an indication of developmental age differences between epiphyses per se; rather, they were used to assess differences between right and left sides of the body, regardless of the stages of active epiphyseal union. Differences in the mean epiphyseal union values for right and left sides were interpreted as bilateral asymmetry.

Analysis

A Kolmogorov-Smirnov test ensured that our asymmetry variables were normally distributed. Paired samples *t*-tests checked for significant differences between right-side and left-side epiphyseal union mean values for each individual. A Wilcoxon signed ranks test assessed the probability of DA. We ran these tests for the sample of 90 individuals, then separately by cemetery sample, then by sex.

RESULTS

Table 1 shows the results of paired samples *t*-tests. We found statistically significant differences in bilateral asymmetry for the sample of 90 individuals ($P < 0.019$). The sample was then tested separately by cemetery, and results of the paired samples *t*-test yielded significant differences in bilateral asymmetry for the early Christian period cemetery sample (n = 36, $P < 0.001$), but not for the late Christian period cemetery sample (n = 54, $P < 0.228$). This finding is consistent with findings from earlier studies on the Kulubnarti Nubians, which demonstrated that early Christian period individuals experienced more environmental stress than late Christian period individuals (Van Gerven et al., 1981; Hummert, 1983; Hummert and Van Gerven, 1983; Sanford et al., 1983; Van Gerven et al., 1985; Moore et al., 1986; Sheridan, 1992; Mittler and Van Gerven, 1994; Sanford and Kissling, 1994). There were no statistically significant differences in bilateral asymmetry between females and males, for the general sample or for each separate cemetery sample (see Table 2).

A Wilcoxon signed ranks test yielded a significant difference in maturation in the right-side epiphyseal union mean values over the left-side epiphyseal union mean values for the overall sample ($P < 0.006$; see Table 3). Out of the 90 comparisons of mean values, skeletal maturation was more advanced on the right side than the left side in 40 cases. In 26 cases both sides were equal; and in 24 cases the left side showed more

TABLE 3. Wilcoxon signed ranks tests for bilateral asymmetry

Sample	RMEAN-LMEAN	N	Mean rank	Sum of ranks	Z	Asymp. Sig. (two-tailed)
Early and Late Christian period	Negative ranks	24[a]	26.08	626.00	−2.770[d]	.006
	Positive ranks	40[b]	36.35	1454.00		
	Ties	26[c]				
	Total	90				
Early Christian period	Negative ranks	7[a]	16.17	323.50	−3.246[d]	.001
	Positive ranks	20[b]	7.79	54.50		
	Ties	9[c]				
	Total	36				
Late Christian period	Negative ranks	17[a]	21.30	426.00	−1.124[d]	.261
	Positive ranks	20[b]	16.29	277.00		
	Ties	17[c]				
	Total	54				

RMEAN, right-side epiphyseal union mean; LMEAN, left-side epiphyseal union mean.
[a] RMEAN < LMEAN.
[b] RMEAN > LMEAN.
[c] LMEAN = RMEAN.
[d] Based on negative ranks.

TABLE 4. Kolmogorov-Smirnov test for normal distribution of asymmetry variables

	LMEAN	RMEAN
N	90	90
Normal parameters[a,b]		
Mean	1.6611	1.7232
SD	1.3145	1.2272
Most extreme differences		
Absolute	.232	.217
Positive	.178	.168
Negative	−.232	−.217
Kolmogorov-Smirnov Z	2.198	2.059
Asymp. sig. (two-tailed)	.000	.000

RMEAN, right-side epiphyseal union mean; LMEAN, left-side epiphyseal union mean.
[a] Test distribution is normal.
[b] Calculated from data.

advanced maturation than the right. While the positive ranks (where right-side epiphyses were more advanced in union than left-side epiphyses) seem to indicate DA, the presence of the negative ranks (where left-side epiphyses were more advanced in union than right-side epiphyses) may indicate FA. Thus, perhaps a combination of DA and FA was occurring in the Kulubnarti Nubians. Moreover a Kolmogorov-Smirnov test (see Table 4) indicated that the variables of bilateral asymmetry were normally distributed, such that the differences found were not likely the result of bias in the sample.

Further statistical tests yielded additional interesting results. When asymmetry was tested separately by cemetery sample, using the Wilcoxon signed ranks test, results were significant for the early Christian period sample, but not for the late Christian period sample (see Table 3). There were no statistically significant differences in asymmetry between females and males. Given that the early Christian period cemetery sample is believed to be the more stressed group, asymmetry appears to be more strongly associated with environmental stress rather than biomechanic factors.

DISCUSSION

Based on results of this study, we suggest that the statistically significant differences found between right-side and left-side epiphyseal union mean values imply asymmetry in growth and maturation. However, this implication should be interpreted with caution. Although our methodology involved the use of four stages to denote the process of epiphyseal union, it is imperative to note that epiphyseal union is a continuous process. Indeed, the precise age or time at which an epiphysis progresses from one stage of union to the next is never seen by the researcher. Therefore, whether or not each of the four stages of union represents a distinct enough growth phase, from the one preceding and or following it, is called into question.

Finding a difference in the stages of union between right-side and left-side epiphyses may not seem meaningful. Yet, recall that Baer and Durkatz (1957) found less variability and less bilateral asymmetry in maturation of hand bone epiphyses than in the onset of ossification of hand bones in normal,

healthy children. Additionally, when our finding of statistically significant bilateral asymmetry in the Kulubnarti skeletons is considered in relation to what earlier research on the Kulubnarti skeletons has shown, the numerical differences between right-side and left-side epiphyseal union stages, and mean values, seem quite meaningful. Earlier research on Kulubnarti skeletons via a variety of methods has supported that environmental stress was greater in the early Christian period cemetery population than in the late Christian period cemetery population. These findings, in conjunction with the statistically significant difference in bilateral asymmetry for the early—but not the late—Christian period cemetery sample support that the four-stage method represents phases of epiphyseal union distinct enough from one another to warrant an interpretation of some sort of asymmetry phenomenon. The cause of the asymmetry, nevertheless, is also debatable.

Previous research has led to suggestions for and debates about the causes of bilateral asymmetry in the skeleton. Roy et al. (1994) suggest a biomechanic cause, relating structure or size to asymmetry. As mentioned earlier, Helmkamp and Falk (1990) allude to age- and sex-related ontogenetic factors as a contributing cause of DA. In their study of rhesus macaque forelimb bones, Helmkamp and Falk (1990) found that DA was significant, with the right-side forelimb bones consistently favored over the left. Further, asymmetry was found to increase with age in females, whereas for males, asymmetry decreased with age. Helmkamp and Falk's study demonstrated that bilateral asymmetry resulting from biomechanic factors can be influenced by variations in age and sex, when relating asymmetry to such features as hand dominance, for example.

Asymmetry exhibited in the form of bilateral differences in skeletal growth and maturation is perhaps a slightly different phenomenon from asymmetry due to biomechanic factors, based on results of our study, explained below. For example, Wong and Carter (1998) propose that, at least for the region of the sternum experiencing high shear stress, skeletal morphogenesis, and growth and development, are accelerated, beginning at a young age. Thus, areas of the skeleton experiencing greater biomechanic stress may grow and mature at a faster rate or at an earlier age. If this were true, then we might expect that both cemetery samples in our study would show significant differences in bilateral asymmetry. Further, given that our overall sample showed more advanced union in the right-side epiphyses over the left, it would seem that this could be explained as due to biomechanic stress relating to hand dominance, where an estimated 90 to 97% of individuals are right-handed (Glassman and Dana, 1992).

When the two cemetery samples were tested separately however, bilateral asymmetry was significant in the early Christian period cemetery sample (the more environmentally stressed group), but not in the late Christian period cemetery sample (the less environmentally stressed group). And, recall that Baer and Durkatz (1957) found no statistically significant asymmetry in maturation of hand bones in their sample of normal, healthy children. It would therefore seem that something other than biomechanic factors was causing the statistically significant difference in asymmetry between the two Kulubnarti samples. We believe when asymmetry is reflected in skeletal maturation (i.e. epiphyseal union), it is caused by environmental stress and not by biomechanic factors.

Moreover, it seems that statistically significant asymmetry in skeletal maturation is absent when environmental perturbations impact the skeleton to a relatively minor degree. Given that both Kulubnarti cemetery samples have been shown to be affected by environmental stress, one group to a greater extent than the other, knowing the threshold where significant asymmetry is likely to result in the form of skeletal maturation is perhaps impossible. At best, the presence of statistically significant bilateral asymmetry in epiphyseal union could show that some higher degree of environmental stress affected the processes of skeletal growth and maturation.

CONCLUSIONS

Bilateral asymmetries in epiphyseal union have been found in a skeletal population

where stress has been previously demonstrated via myriad methods of analysis. The benefit of bilateral asymmetry in epiphyseal union as a method of assessing stress is that it may be possible to detect asymmetry in bones where none exists in the dentition, or where interpretations from the dentition are limited (Greene, 1984). Thus, the absence of dental metric asymmetries, or lack of sufficient interpretations of dental metric asymmetries, does not preclude the possibility of environmental stress exhibiting itself in other forms of asymmetry, such as in the form of bilateral differential development (epiphyseal union).

The method presented in this study is useful for detecting stress in teenage skeletons—individuals too old in some cases to show evidence of past, childhood stress (e.g. cribra orbitalia which may have healed over, or linear bone growth retardation). The absence of childhood indicators of stress in teenage skeletons may yield misleading interpretations, such as the idea that stress was greater during early childhood but not through the teenage years. Finally, results of this study suggest that statistically significant bilateral asymmetry is not exhibited in the skeletal maturation of teenagers and young adults, except when there is perhaps a pronounced degree of environmental stress.

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